A PROPOSED RECLASSIFICATION OF THE GASTROPOD FAMILY VERMETIDAE

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ABSTRACT

Because of their widespread occurrence in the intertidal zones of warm-temperate to tropical seas and their peculiar adaptations, the Vermetidae could become useful to the marine ecologist if they were readily identifiable in the field. The present paper is an attempt to show what characteristics are most constant and useful in recognition, to review the nomenclatural history of the group, and to indicate something as to the geographic distribution of species. In the revised classification, five genera, with five additional subgenera, are recognized. Brief lists of the species that may be assignable to each are given, although these must remain tentative until detailed studies are made by students who have access to properly collected material.

In this paper, *Tripsycha* is proposed as a new genus; *Siphonium lituella* Mörch is selected as the type species of *Dendropoma* Mörch, *Serpulorbis polyphragma* Sassi as that of *Thylacodes* Mörch, and *Bivonia contorta* Carpenter as that of *Thylacodus* Mörch and of *Thylaeodus* Mörch; and lectotypes are selected for *Vermetus adansonii* Daudin, *V. afer* Gmelin, *Bivonia contorta* Carpenter, *B. c.* var. *indentata* Carpenter, *Petaloconchus macrophragma* Carpenter, *Siphonium* (*Dendropoma*) *leucozonias* Mörch, and *Siphonium* (*D.*) *lituella* Mörch.

A. INTRODUCTION

The Vermetidae (worm gastropods) probably hold a record among molluscs for the degree of confusion they have promoted, both in collections and in the literature; for they have been misconstrued at every level from subspecies to phylum. An attempt is made here to point out objective criteria for separation of groups within the family. A complete monograph of the species, however, must wait until field observations have confirmed or disproved laboratory analyses of seeming differences.

Although in many parts of the world—especially in the tropics—the vermetids are abundant intertidal organisms, they have never been popular with collectors. Properly recognized, they could become, on account of their peculiarities in habit and distribution, useful indicators for the ecologist in the description of intertidal zones. Most of the few papers on the family deal with anatomy and physiology of the animals or with local faunas. We still lean upon the systematic reviews by two

authors whose works were published a century ago : Carpenter (1857*b*), for a monograph of the genus *Petaloconchus*, and Mörch for, first, a tentative classification of the family (1859–60*a*) and then (apparently after a survey of the extensive Hugh Cuming Collection) a review of the species (1861–62*b*). His second arrangement differs at many points from the first one. Conceptual tools for the study of variation had not been worked out in Mörch's time. Small wonder, then, that in trying to cope with some of the most variable of gastropods he finally resorted to a naming system so complex and confused that Carpenter (1864 : 558, footnote) later dismissed it as a "posture of binomial nomenclature". Indeed, one now concedes that, useful as Mörch's work may be in a general way, we must, under modern rules, reject many of the new names he proposed, for all those below specific rank are polynomial and inconsistent. Citation by Tryon (1886) and reprinting by Clessin (1901–04) were not in a form that would validate any of them.

Both Mörch and Carpenter relied upon the adult shells alone for their classifications. Perhaps neither had an adequate microscope, for they both missed some conspicuous features in the nuclear whorls, and Mörch saw structures in certain opercula that later research has failed to confirm.

The first step in a fresh study of the family is to define its limits and to exclude what does not properly belong. Tubicolous annelid worms are frequently confused with vermetids. Some of these worms do build irregularly coiled tubes, but on close inspection one sees that the tubes are lustreless and of two-layered construction, either beginning with a non-coiled initial chamber or open at the posterior end. The genera *Burtinella*, *Discovermetulus*, *Lemintina*, *Serpula*, *Spirorbis*, *Tubulostium* and *Vermilia* may be rejected without hesitation, for their type species are now generally recognized as annelids. Although from time to time authors have listed *Caporbis*, *Segmentella*, *Serpulus*, *Stoa*, and *Spiroglyphus* as gastropods, these groups also should probably be classed as annelids. At the family level, the Vermetidae have been traditionally associated with *Vermicularia*, a group that Morton (1953) has shown to be related rather to Turritellidae, for the juvenile shell is coiled in much the same general plane as the later whorls. *Stephopoma* and *Siliquaria*, also with turritelloid apices, belong near *Vermicularia*.

Remaining in Vermetidae, then, are those forms, solitary or colonial, in which the juvenile snail, upon emergence from the capsular membrane and the protection of the parent's tube, attaches itself to a favourable substrate and begins coiling its adult shell around an axis at a 90° angle to that of the larval shell. Several named genera may be recognized, combining differences in anatomical and shell structures, manner of coiling, and habits. The present paper will attempt to subdivide the restricted family Vermetidae in terms of the hard parts and general external aspects, while a paper by Dr. Morton, to be published later, will discuss differences in anatomy and feeding patterns.

The Vermetid Shell

An isolated section of a vermetid tube is nearly useless for specific or even generic determination, but texture and structure may indicate its placement within the family. The shell is three-layered, with an inner layer that is glossy and porcel-

lanous, mostly white or tinged with some shade of brown. The middle layer is less distinctive but thicker than the other two, and the outer layer carries whatever sculpture is present, its colour ranging from white through buff or pink to brownish black. Sculpture may be either longitudinal or transverse. The irregular coiling of the shell makes the use of such terms as " spiral " and " axial" ambiguous. Full expression of sculpture may be inhibited by such factors as crowding, rate of growth, and unfavourable environment, which adds to the problems of recognition. Several writers have commented on the frequent sealing off of the early whorls, especially if the shell has been broken. The posterior part of the mantle is capable of secreting a convex septum that closes off either an unneeded or a broken portion of the tube, and in some specimens this sealing may be repeated at close intervals. In one genus (*Petaloconchus*) one or more spiral laminae or shelves may encircle the columella throughout the medial whorls.

The Operculum

The operculum is a spirally-wound plate of chitin. At its most complex development it is thickened at the centre, with a button-like scar on the inner surface, the spiral so tightly appressed as to seem nearly flat. An intermediate or simple form of operculum shows only a few turns, the whole structure reduced in size to half or less of the diameter of the aperture, with spirals that stand up as coiled laminae on a saucer-shaped base. One group of the vermetids (*Serpulorbis*) has dispensed with the operculum entirely. Correlations of opercular patterns with feeding habits will be discussed by Dr. Morton.

The Nuclear Whorls

Few gastropods are adapted to a sessile existence. Perhaps this accounts for the vermetids having developed a special means for the newly-emerged young to cement their shells to the substrate without becoming imprisoned in the process. The larval shell is comprised of two to four normal-appearing whorls except that the aperture is either twisted forward or provided with a sinuous or almost clawlike outer margin. So shaped, the shell can lie firmly against the substrate while the animal continues both feeding and the formation of the next volutions of the shell, which encircle the juvenile shell on an axis of coiling 90° different from that of the initial whorls. This is reminiscent of the submerged nucleus in Architectonicidae, to which group the Vermetidae may be related.

Nuclear whorls may be found in three ways : (*a*) By scanning the underside of a colony or an individual coil broken loose from the substrate ; (*b*) by inspecting the outer surfaces of adult tubes—especially crevices near the apertures—for newly-emerged young that creep down the outside of the parent's tube and attach in the first protected niche they encounter ; (*c*) by extracting the soft parts from adult tubes (especially from those that have been quickly dried after collection or preserved in neutral alcohol) for the young or larval shells that may still be sheltered in the mantle cavities of the adults. With practice one soon learns to recognize the newly-attached young, which may be detected even with a small hand-lens. At first glance they look like a plump little wheel of an automobile, with a shiny central cap.

Under higher magnification, differences become apparent, as one compares the young of groups here called genera for size, number of nepionic whorls, colour, and relative shape.

Habits of Growth

It is impossible to arrive at any generalizations as to growth patterns that will apply to every contorted mass of vermetids that one finds. Nor is it even possible to identify every such mass, a fact that accounts in part for the unpopularity of the family with collectors. However, there are some features for which one should watch. Are the tubes entrenched in the substrate or slotted into each other where one overrides another? Is coiling rather regularly planorboid during the earlier part of the adult whorls? Are the whorls uniformly small and coiled like a "*Turritella* squeezed sideways"? Are there fairly regular scars of broken tube ends, where a vertical feeding tube has been abandoned and replaced by one taking off at a different angle? It is this sort of pattern that may give a clue as to generic placement, but confirmation should be sought in the other characteristics. One group, *Petaloconchus*, has an internal structure that is a sure clue—spiral laminae of complex form that project into the tube from the columellar wall. The function of these structures is yet open to investigation. Another problem that remains for future solution is the relationship between form of shell and the degree of crowding in colonies. Is solitary versus colonial development a specific character? Or do isolated individuals producing young inevitably form a tight-knit colony? No one has yet performed the observational experiments that would give the answer, or at least no published record has come to our attention.

Some of the early authors, especially Mörch and Carpenter, thought that many vermetids were sinistrally coiled, but this seems to be a matter of faulty observation, for no sinistral specimens have been seen during the course of the present study, which has involved scrutiny of hundreds of specimens over a period of some ten years. Probably the 90° change of angle, which they failed to note, may have led to this impression. Also, they, like other authors, may have mistaken specimens of *Spirorbis*, an annelid worm that coils either way, as vermetids.

B. NOMENCLATURAL UNITS IN VERMETIDAE

The generic and subgeneric names that have been, with some plausibility, applied to members of the family Vermetidae are arranged here in alphabetical order (except for the type genus, *Vermetus*, which is considered first), with references, statement of type species, and discussion of any nomenclatural problems involved. Names available within the family are in bold face type.

Vermetus Daudin, 1800 : 34.

Type species (absolute tautonymy) : *V. adansonii* Daudin, 1800 [based on "Le Vermet" of Adanson, 1757].

The status of this name is somewhat equivocal and will remain so unless it is placed on the Official List of Generic Names by the International Commission on Zoological Nomenclature. Some authors have tried to avoid the difficulties implicit

in Daudin's proposal by crediting the name to Cuvier, 1800, but his usage is as an absolute *nomen nudum*, without description or mention of any species. Daudin cited six species that had been described by Adanson, but he gave no formal bibliographic reference to Adanson's publication. On this ground one could justifiably disregard *Vermetus* Daudin and credit the name to the next author who fulfilled the requirements of publication. A substantial barrier stands in the way of this, however, for Daudin at the same time described, in an acceptable manner, four new species that he assigned to *Vermetus*. Although he cited the group as belonging in Gastropoda, every one of his four new species, as the illustrations show, are tubicolous annelids. Therefore, if *Vermetus* as a name cannot be tied to one of the cited Adanson species (all but one of which are molluscan), the name must be transferred to the Annelida, where it would either fall as a synonym or jeopardize some later-established name. In the interests of stability, it seems wisest to be a little lenient, by interpreting Daudin's obvious intention as having been fulfilled. Following is an exact transcription of Daudin's proposal:

"Genre Vermet. Vermetus. Adanson
Vermicularia. Lamarck.

"Caractère générique. Coquille tubulée, tortillée en spirale irrégulière, ordinairement adhérente, et garnie d'une ouverture orbiculaire et operculée.

"Ce genre déja formé par Adanson dans son histoire des coquilles du Sénégal, et confondu par les autres naturalistes et par Bruguière même avec les Serpules, est formé par un gastéropode voisin de celui des planorbes par ses deux tentacules en languette, munis d'un oeil à leur base extérieure; mais il en diffère essentiellement par sa bouche prolongée en une trompe cylindrique garnie de plusieurs rangées de dents crochues, et de plus par un opercule rond très-mince qu'il peut retirer avec lui dans l'intérieur de son tube. Il reste toujours dans la même place, parce que le tube qu'il habite est attaché sur les rochers et sur des coquilles.

"Adanson a décrit les six espèces suivantes.

1. Vermet d'Adanson. *Vermetus Adansonii.*
   Serpula lumbricalis Linn.
2. Vermet musier. *Vermetus arenarius.*
   Serpula arenaria Linn.
3. Vermet Datin. *Vermetus afer.*
   Serpula afra Gm.
4. Vermet Dofan. *Vermetus Goreensis.*
   Serpula Goreensis Gm.
5. Vermet Lispe. *Vermetus glomeratus.*
   Serpula glomerata Linn.
6. Vermet Jélin. *Vermetus intestinalis*
   Serpula intestinalis Gm."

Examining the work by Adanson that Daudin obviously meant—the *Histoire naturelle de Sénégal, Coquillages* (which, being published in 1757, does not itself qualify as a source of generic names)—one finds on page 160 the description of "Le Vermet".

This is the only form so termed by Adanson, although his other five species were described in close association with it and evidently were considered to belong in the same group. I believe that one may interpret Daudin's statement, "Vermet d'Adanson. *Vermetus adansonii*" as fixing the type of *Vermetus* by absolute tautonymy under the current definition of that term in the International Code. The first subsequent designation of the type of *Vermetus* is by Gray (1847), who selected *Serpula lumbricalis* Linné. This would make *Vermetus* an objective synonym of *Vermicularia* Lamarck, 1799. [One may remark that Daudin's citation of Lamarck's species as a synonym perpetuated a common confusion of early authors.] Acceptance of absolute tautonymy as the mode of type fixation for *Vermetus* seems to be the only possibility for retaining the name in its accustomed sense.

Aletes Carpenter, 1857*a* : 226 [not *Aletes* Carpenter, 1857*c* : 301].

Type species (monotypy) : *A. squamigerus* Carpenter, 1857.

Carpenter included the name *Aletes*, as a new subgenus of *Siphonium*, in two manuscripts on which he was working. By the fortunes of publication, the one that carried only a partial diagnosis appeared first, and the only species cited by name therein was of a form described as new that he himself later recognized (Carpenter, 1864 : 654) not to be congeneric with the species he had used as basis for his subgeneric description, *Vermetus centiquadrus* Valenciennes. The latter is, in fact, the only species discussed by Carpenter that fits his diagnosis, "*Operculo parvum concavo, multispirali, fere ut in* Turritella *formato*", and it was selected as type of *Aletes* by Clessin in 1902. My earlier attempt (Keen, 1958 : 297), to preserve Carpenter's intended usage by using the signature dates of what seemed to be an earlier private edition issued by Carpenter, now seems ill-advised in view of evidence published by Iredale (1916 : 36) that I had not considered sufficiently. As Iredale demonstrated, Carpenter's edition was instead a later re-issue of the British Museum official publication. These signature dates must therefore be regarded as dates of printing rather than dates of release to the public.

The species *A. squamigerus* is non-operculate, and the shell is so similar in form to that of the type of *Serpulorbis* that we can hardly maintain *Aletes* as a morphologically distinct group with it as type. The only way the generic name could be salvaged for use in the West American fauna would be to petition the International Commission on Zoological Nomenclature that *Aletes* be made a *nomen conservandum*, with *A. centiquadrus* as type. One might argue that Carpenter's mis-allocation of his new species to *Aletes*, which he himself later rejected, might constitute a form of misidentification, and one could thus ask to have *Aletes* preserved. However, one would be on rather insecure ground in trying to prove that this is the accustomed sense in which the generic name has been used, for a census of the literature would be most apt to show that the combination "*Aletes squamigerus*" has appeared more frequently than the combination "*A. centiquadrus*". Also, such action is a matter that would require several years of time. At present, it seems better to let *Aletes* lapse into synonymy and to place *Vermetus centiquadrus* in *Vermetus*, *s. l.*, until material is available for a careful study of soft parts and nuclear whorls, neither of

which have been described. The one operculum illustrated here (figs. 2–3) is distinctive, and if additional material proves similar, a separate generic category for this species would surely seem justified.

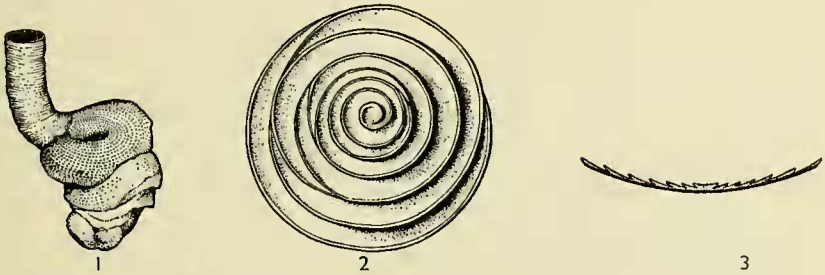

Fig. 1. *Vermetus centiquadrus*. Stanford Univ. specimen, West Mexico. ×½.
Fig. 2. Same, operculum, full view. ×9.
Fig. 3. Section of operculum to show laminae. ×9.

Anguinella Conrad, 1845–46 in 1838–61 : 77. [Not *Anguinella* Van Beneden, 1845.]
Type species (monotypy) : *Serpula virginica* Conrad.

Bivonia Gray, 1847 : 156. [Not *Bivonia* Cocco, 1832.]
Type species (original designation) : *Vermetus glomeratus* Bivona-Bernardi, 1832.

Cladopoda Gray, 1850 : 83.
Type species (subsequent designation, Tryon, 1886) : *C. grandis* Gray, 1850 [based on " *Vermetus arenarius* " of Quoy & Gaimard, not Linné].

Cryptobia Deshayes, 1863 : 65. [Not *Cryptobia* Leidy, 1846. Probably not a mollusc.]

Dendropoma Mörch, 1861 : 153.
Type species (here designated) : *Siphonium* (*D.*) *lituella* Mörch, 1861.

Dofania Mörch, 1860*a* : 34.
Type species (subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1884) : Le Dofan Adanson = *Serpula goreensis* Gmelin, 1791.
Adanson's type specimen of Le Dofan seems no longer to be discoverable, according to Fischer-Piette (1942 : 264). As the type figure does not permit of specific determination, the generic name is at present unusable.

Elliptovermetus Cossmann & Peyrot, 1922 : 69.
Type species (original designation) : *Vermetus breigneti* Cossmann & Peyrot ; Aquitanian (Upper Oligocene) of France.

Hatina Gray, 1847 : 156.
Type species (monotypy) : " *Verm. inoperculatus* " [apparently an error for *Vermetus inopertus* Rüppel & Leuckart, 1830–31].

This is probably a synonym of *Serpulorbis*, but uncertainty as to the name of the type species suggests that it be classed as a *genus dubium*.

Macrophragma Carpenter, 1857*b* : 308.
Type species (absolute tautonymy) : *Petaloconchus macrophragma* Carpenter, 1857.
The name was only tentatively proposed by Carpenter but was accepted by Mörch in 1861, so that it is available for use.

Magilina Vélain, 1877 : 105.
Type species (monotypy) : *M. serpuliformis* Vélain.

Novastoa Finlay, 1927 : 386.
Type species (original designation) : *Siphonium lamellosum* Hutton, 1873.

Petaloconchus Lea, 1843 : 233.
Type species (monotypy) : *P. sculpturatus* Lea ; Miocene of Virginia.

Polyphragma Vaillant, 1871 : 189. [Not *Polyphragma* Quatrefages, 1866.]
Type species (monotypy) : *Vermetus varians* Orbigny, 1841.

Scolissedium "Rein." Verany, 1846 : 15. Evidently an erroneous spelling of *Scolixedion*, q. v.

Scolixedion Renier, 1807, of authors. Invalidated by the International Commission (I.C.Z.N., 1957), and placed on the "Official Index of Rejected Generic Names" (I.C.Z.N., 1958).

Serpuloides Gray, 1850 : 83. [Not *Serpuloides* Murchison, 1839.]
Type species not selected.

Serpulorbis Sassi, 1827 [also recorded as Sasso] : 482.
Type species (monotypy) : *S. polyphragma* Sassi = *Serpula arenaria* Linné, 1758.
The generic name has been misspelled as *Serpulopsis* by some authors.

Siphonium Gray, 1847, of authors [not *Siphonium* Link, 1807] = *Vermicularia*.

Siphonium "Browne" of Mörch, 1859 : 348, 353 [not of Link, 1807] = *Dendropoma*.

Spiroglyphus Daudin, 1800 : 39.
Type species (subsequent designation, Mörch, 1861) : *S. annulatus* Daudin.
Daudin described the shells of two species, without being sure whether they were worms or molluscs. He cited the type locality of *S. annulatus* as the Indian Ocean, on Fissurellas and Patellas. His principal distinction for the genus was that it corrodes a channel for itself. His type figure is of an irregularly coiled shell on what looks to be a Caribbean *Diodora*, which has led some authors to reinterpret the type locality. There are some tube-dwelling worms that resemble his figure, although they may not truly corrode a channel as one group of vermetid gastropods do.

Dr. Olga Hartman, specialist on Annelida, to whom a photograph of Daudin's figure was submitted, could not positively identify the form either as an annelid or as not an annelid. I feel the same hesitation about saying definitely whether or not the figure represents a vermetid gastropod. Hence, we would need some objective basis other than the figure before we could accept the name *Spiroglyphus* as valid in Vermetidae. Rediscovery of Daudin's type specimen might solve the problem, but inquiries in France have brought no clues. Dr. E. Fischer-Piette, in fact, reported that he would not even know where to start a search. Another possibility would be the selection of a neotype, a course acceptable under the International Rules and one which I had planned to adopt, but I have found no specimen in the collections available (including that storehouse of malacological treasures, the British Museum of Natural History) that would satisfy the necessary requirements. The name *Spiroglyphus* has been widely used in the Gastropoda—true—but it has also been used by some palaeontologists, probably incorrectly, for the annelid group of *Tubulostium* Stoliczka, 1868, or *Rotularia* Defrance, 1827. For the present, therefore, it seems advisable to set it aside as a *genus dubium* until such time as it can be given unequivocal status with a type species based on a recognizable specimen, either by rediscovery of Daudin's material or by finding an acceptable neotype—both possibilities now seeming rather unlikely.

Tetranemia Mörch, 1859 : 353.

Type species (monotypy) : *Serpulus* (*T.*) *dentiferus* (Lamarck) of Quoy & Gaimard (not of Lamarck) = *Thylacodes* (*T.*) *longifilis* Mörch, 1862.

Thylacodes Agassiz, 1846 : 370, 381. *Nomen nudum.*

Thylacodes Mörch, 1862 : 64 (*ex* Guettard, 1774, non-binomial).

Type species (here designated) : *Serpulorbis polyphragma* Sassi, 1827 = *Serpula arenaria* Linné, 1758.

Thylacodus Mörch, 1860*b* : 77 (July).

Type species (here designated) : *Vermetus contortus* (Carpenter) = *Bivonia contorta* Carpenter, 1857.

Other species included by Mörch : *V.subcancellatus* Bivona-Bernardi, *V. conicus* Dillwyn, and *V. contortus* var. *indentatus* Carpenter.

Thylaeodus Mörch, 1860*a* : 48 (January).

Type species (here designated) : *Vermetus contortus* (Carpenter) = *Bivonia contorta* Carpenter, 1857.

Mörch proposed the name in a postscript to his first paper, as follows : " Enfin, je proposerai le nom de *Thylaeodus* pour les Vermets sans plis. " As it stands, this seems too vague to be a valid proposal, but careful reading of the paper, especially page 39, shows that he would include these species in the category of vermetids without folds : *V. contortus* and its variety, *V. albidus* Carpenter ; *V. subcancellatus* Bivona-Bernardi ; and *V. carinatus* Quoy & Gaimard. One may suspect that the spell-

ing "*Thylaeodus*" was a printer's error, for in the subsequent paper, where more formal treatment was given, the spelling was consistently "*Thylacodus*". However, under the International Rules, the original spelling must be accepted unless evidence in the paper itself demonstrates an error. Mörch having given no clue as to derivation, we must adopt *Thylaeodus* as the valid spelling. In a way this is advantageous, for thus we avoid the confusion of *Thylacodus* with *Thylacodes*, names used by Mörch in different senses.

Veristoa Iredale, 1937 : 254.

Type species (original designation) : *V. howensis* Iredale.

Vermiculus Mörch, 1859 : 348 (*ex* Lister). [Not *Vermiculus* DaCosta, 1776 nor Linck, 1783.]

As of Mörch, this is a synonym of *Vermicularia*. The name is a pre-Linnean term, used non-binomially by later authors for a mélange of forms. The earliest such use is by DaCosta for three unnamed species, one of which is a *Serpulorbis*. It would seem to serve no useful purpose and should be placed on the Official Index of Rejected Generic Names.

Vermitoma Kuroda, 1928 : 40.

Type species (monotypy) : *V. luchuana* Kuroda (*ex* Hirase MS.). [Description in Japanese.]

C. REVISED CLASSIFICATION OF THE VERMETIDAE

Generic synonymies, as now understood, are given below, with notes on shell morphology and lists of the species that, with some confidence, one may assign to each group. Citations are, in the main, only to author and date but full references for many species are given in Section D.

Family VERMETIDAE Gray, 1828

Sessile gastropods with shells more or less firmly attached throughout life to rock or to other shells ; coiling irregular to disjunct (lax) ; axis of coiling of nuclear whorls at a right angle to that of later whorls ; operculum chitinous, spiral, with a tendency toward external laminae.

Genus ***VERMETUS*** Daudin, 1800

? *Dofania* Mörch, 1860.

Mainly solitary or in small clusters, coiling usually irregular ; columellar wall smooth, without laminae ; nuclear whorls two, globose to elongate ; operculum thin, spiral, one-half or less the diameter of the aperture.

Subgenus ***VERMETUS***, *s. l.*

Into this category must be grouped all the otherwise unassignable species—those described on the basis of incomplete shells, those of unknown provenance, and those

not yet studied in adequate detail. The major part of some 250 named forms, fossil and living, fall herein.

Subgenus ***VERMETUS***, *s. s.*

(Text-figs. 4–7)

Coiling irregular but shell mostly well attached; without feeding-tube scars; colour, brown; operculum small, less than half the diameter of the aperture, consisting of a concave disc with a spiral lamina of one to two turns (Text-figs. 6–7); nepionic shell of two subglobular whorls (Text-fig. 5).

Until recent years (Fischer-Piette, 1942), the type material of *V. adansonii* was lost to science. In the meantime, authors had misdetermined the species and confused it with a *Petaloconchus* (*Macrophragma*) from other parts of West Africa. That the type species of *Vermetus* does not show any internal spiral laminae is

4 5 6 7

FIG. 4. *Vermetus adansonii*, lectotype, after Fischer. ×0·75.
FIG. 5. Nuclear whorls of *V. adansonii*, topotype. ×30.
FIG. 6. Same, operculum full view. ×35.
FIG. 7. Oblique view of operculum as seen on dried animal. ×35.

confirmed both by the original material (Fischer-Piette, 1942, pl. 9, figs. 3–5) and by topotype specimens.

Assignable species:

V. (*V.*) *adansonii* Daudin, 1800 [type species]. West Africa, especially Sénégal.
V. (*V.*) *afer* (Gmelin, 1791). West Africa, especially Sénégal.
V. (*V.*) *triqueter* (Bivona-Bernardi, 1832). Mediterranean.

Subgenus ***THYLAEODUS*** Mörch, 1860*a* (January)

(Text-figs. 8–11)

Bivonia of authors, not of Gray, 1847; *Thylacodus* Mörch, 1860*b* (July).

Buff to brown shells of moderate or small diameter, with strongly cancellate to beaded sculpture; feeding-tube scars (abandoned remnants of former vertical tubes) present on most specimens; operculum one-half to three-fourths the diameter of the aperture, with a spiral lamina of chitin that rises free from the disc.

These shells have been grouped by many authors, following Carpenter, in the genus *Bivonia*, but this is untenable on two counts: the name is preoccupied and the type species differs in several significant features. Though resembling *Petaloconchus* externally, this group consistently lacks the internal spiral laminae and thus is closer to *Vermetus*, *s. s.*

Assignable species :

V. (*T.*) *contortus* (Carpenter, 1857) [type species]. Tropical West America.
V. (*T.*) *indentatus* (Carpenter, 1857). Tropical West America.
V. (*T.*) *?quoyi* (H. & A. Adams, 1854). Indo-Pacific.
V. (*T.*) *semisurrectus* Bivona-Bernardi, 1832. Mediterranean.

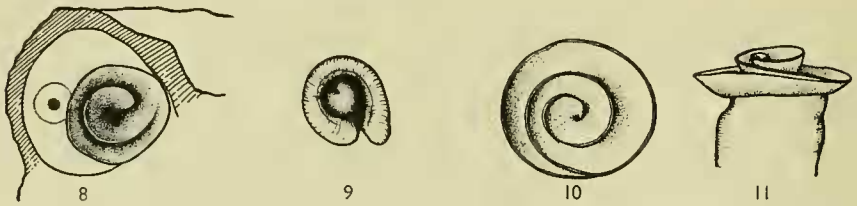

Fig. 8. *V.* (*Thylaeodus*) *contortus*, showing operculum in place in a broken aperture. Topolobampo, West Mexico. ×12.
Fig. 9. *V.* (*T.*) *contortus*, apex of nuclear whorls, as seen from attached side, showing also the first subsequent whorl. ×12.
Fig. 10. *V.* (*T.*) *indentatus*, operculum, full view. Guaymas, West Mexico. ×17.
Fig. 11. Same specimen, side view of operculum. ×17.

Genus ***SERPULORBIS*** Sassi, 1827

Lemintina of authors (not of Risso, 1826) ; *Anguinella* Conrad, 1846, preoccupied ; *Hatina* Gray, 1847 ; *Serpuloides* Gray, 1850, preoccupied ; *Aletes* Carpenter, 1857*a* ; *Tetranemia* Morch, 1859 ; *Thylacodes* Mörch, 1862*b*.

Shells among the largest of the family, the coiling of roughly concentric loops, especially in the early whorls, the later coiling in colonial forms being densely contorted, lax, or hardly apparent. Scars of broken feeding tubes apparent on most specimens. Colour of shells ranging from dark brown to pure white. Nuclear whorls lighter in colour than the rest of the shell, of two to four whorls, globose-conic rather than cylindrical. Operculum wanting.

Subgenus ***SERPULORBIS***, *s. s.*

(Text-figs. 12–14)

Colonial forms, in the main, with tubes that are concentrically looped in the young to weakly contorted in the adult ; sculpture of spiral lines variously intersected to form nodes or scales.

Assignable species :

S. (*S.*) *arenaria* (Linné, 1758). Mediterranean. (Synonyms : *S. polyphragma* Sassi, 1827 [type species] ; *Vermetus gigas* Bivona-Bernardi, 1832.)
S. (*S.*) *decussatus* (Gmelin) [*Serpula*]. Caribbean.
S. (*S.*) *cruciformis* (Mörch, 1862) [*Thylacodes*]. West Mexico.
S. (*S.*) *masier* (Deshayes, 1843) [*Vermetus*]. West Africa.
S. (*S.*) *medusae* (Pilsbry, 1891) [*Thylacodes*]. Japan.

S. (*S.*) *novaehollandiae* (Chenu, 1843, *ex* Rousseau MS) [*Vermetus*]. ?Australia.
S. (*S.*) *sipho* (Lamarck, 1818) [*Serpula*]. Indo-Pacific.
S. (*S.*) *squamigerus* (Carpenter, 1857) [*Aletes*]. California.
S. (*S.*) *validus* Kuroda & Habe, 1952. Japan.

This group seems to have appeared earliest in time of the vermetids, as early at least as Eocene time : for example—among others—*S. morchi* and *S. cancellatus* Deshayes, 1861, from the lower and middle Eocene of Europe, and *S. chavani* Harris & Palmer, 1946, from the upper Eocene of south-eastern United States. Some Upper Cretaceous forms have a pattern of coiling that seems *Serpulorbis*-like—as in *S. lamellosus* (Stoliczka, 1868), from India—although the preservation is not complete enough to provide indisputable evidence that these are gastropods and not tubicolous annelids.

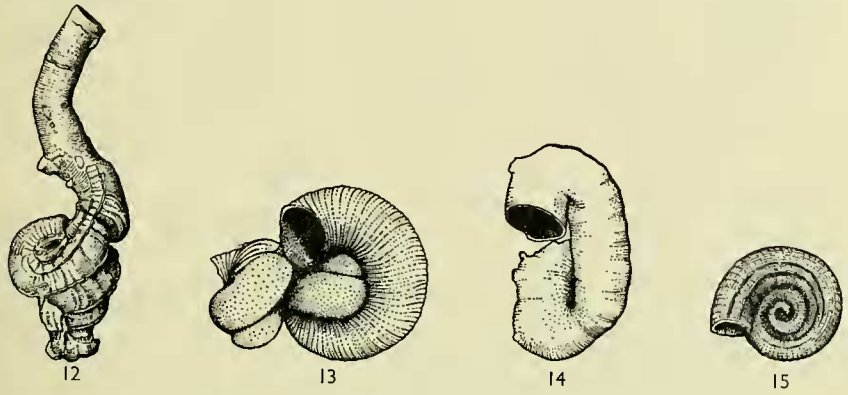

FIG. 12. *Serpulorbis arenarius* (Linné), after Monterosato. Mediterranean. ×½.
FIG. 13. *S. arenarius*, nuclear whorls. Sicily (Stanford Univ. collection). ×22.
FIG. 14. *S. polyphragma*, shell, after Priolo. ×½.
FIG. 15. *S.* (*Cladopoda*) *grandis*, shell, after Quoy & Gaimard, somewhat modified from specimens. Indo-Pacific. ×½.

Subgenus ***CLADOPODA*** Gray, 1850

(Text-fig. 15)

Coiling planorboid throughout life (rarely lax) ; shells mostly solitary rather than colonial, large in diameter, with the entire coil in contact with the substrate ; colour of shell ivory white to blackish brown ; sculpture of longitudinal threads that are but weakly intersected by transverse sculpture.

Assignable species :

S. (*C.*) *colubrinus* (Röding, 1798) [*Serpula*]. Indo-Pacific area. (Synonym : *V. ater* Chenu, 1844.)
S. (*C.*) *grandis* (Gray, 1850) [type species : as *Cladopoda*]. Indo-Pacific.
S. (*C.*) *imbricatus* (Dunker, 1860) [*Vermetus*]. Japan.
S. (*C.*) *margaritaceus* (Chenu, 1844, *ex* Rousseau MS.) [*Vermetus*]. Probably West Mexico. (Synonym : *V. margaritarum* Valenciennes, 1846.)

Genus *TRIPSYCHA*, new genus

(Text-figs. 16–20)

Type species : *Vermetus tripsycha* Pilsbry & Lowe, 1932. West Mexico.

White shells of moderate size, with the early whorls firmly attached and coiling as in *Serpulorbis* ; medial and later whorls mostly unattached and coiling in hollow cone form, somewhat as in *Petaloconchus, s.s.* ; last whorl lax and uncoiled. Operculum slightly concave, with an appressed spiral lamina of several volutions. Nuclear whorls unusually large, with several turns, rather more elongate than in most vermetids except some *Petaloconchus* (*Macrophragma*). Mainly solitary shells, but when crowded they may form a radiating cluster of tubes, due to the tendency of each individual to grow away from any nearby competitor.

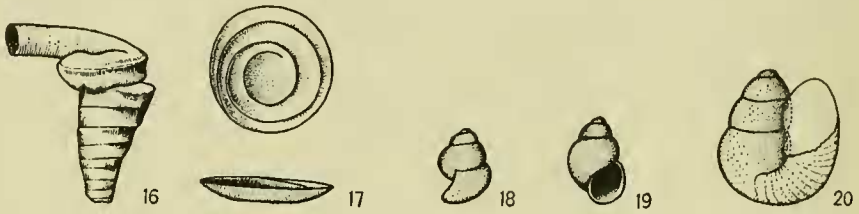

Fig. 16. *Tripsycha tripsycha*, holotype, after Pilsbry & Lowe ; Guyamas, Mexico. ×½.
Fig. 17. *T. tripsycha*, operculum, full and side views. Stanford Univ. collection. Guaymas. ×5.
Fig. 18. Same, nuclear whorls, side view ; from brood capsule. ×15.
Fig. 19. Same specimen as Fig. 18, apertural view. ×15.
Fig. 20. Nuclear whorls, after attachment to substrate. Stanford Univ. collection, Guaymas. ×17.

The name of the subgenus is that of the type species, as this seems to be a very suitable noun coined by Pilsbry & Lowe from the Greek words *tri* and *psyche* and evidently intended to convey the meaning, " of three minds ", in reference to the three modes of coiling during the life of the individual.

Assignable species :

T. tripsycha (Pilsbry & Lowe, 1932). West Mexico.

Genus *PETALOCONCHUS* Lea, 1843

Petaloconcha, unjustified emendation by Cossman, 1912.

Coils forming a hollow cylinder, at least in the young ; medial whorls with a more or less complex internal structure of spiral laminae projecting from the columellar wall.

Subgenus *PETALOCONCHUS*, *s. s.*

(Text-fig. 21)

Last whorl lax or unwound, earlier whorls forming a symmetrical hollow cone. Nuclear whorls and operculum unknown. Sculpture, when present, evenly cancellate.

The type species was described from the Miocene of the eastern United States. A few closely related species have since been described, all in the Middle Tertiary of the Caribbean area. The subgenus in the strict sense is not recorded elsewhere.

Assignable species :

P. (*P.*) *sculpturatus* Lea, 1843. Miocene, Virginia [type species : holotype refigured, Gardner, 1947, pl. 55, fig. 21]. (Synonym : *P. domingensis* Sowerby, 1849.)

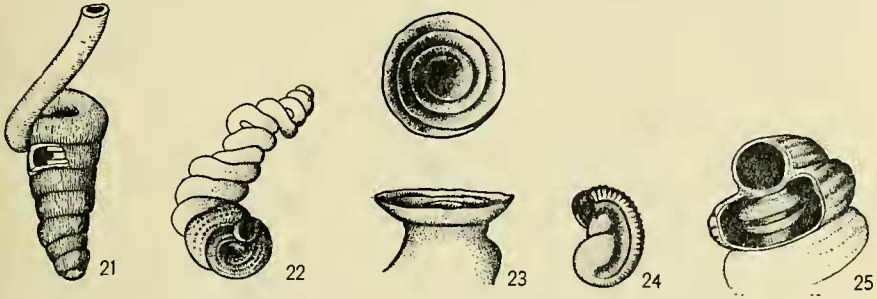

FIG. 21. *Petaloconchus sculpturatus*. Specimen, Stanford Univ. collection, from the Miocene of Trinidad, with internal laminae showing in the broken section of one coil. ×½.

FIG. 22. *P.* (*Macrophragma*) *macrophragma*, sketch of lectotype, to illustrate coiling. Mazatlán, Mexico. ×2. B.M. (N.H.) Reg. No. 57.6.4.1500.

FIG. 23. *P.* (*M.*) *macrophragma*. Operculum. Stanford Univ. collection. ×13.

FIG. 24. Same, nuclear whorls. West Mexico. ×12·5.

FIG. 25. Detail of columellar laminae. Stanford Univ. collection, Oaxaca, Mexico. ×6.

Subgenus ***MACROPHRAGMA*** Carpenter, 1857

(Text-figs. 22–25)

Polyphragma Vaillant, 1871 [not Quatrefages, 1866] ; *Petaloconchus, s. s.* of authors.

Coiling regular, especially in the early whorls, described by Carpenter as "like a *Turritella* squeezed sideways". Sculpture cancellate, but with the longitudinal ribs tending to be predominant and sub-carinate.

Nuclear whorls two to four, ivory white to waxy yellow, conic to cylindrical. Adult shell medium to dark brown in colour. Operculum concave, with an upstanding spiral lamella of one or two volutions, diameter less than that of the aperture, resembling that of *Vermetus* (*Thylaeodus*) in form.

The shells are either solitary or colonial and are mostly smaller in size than in other vermetid groups except *Vermetus* (*Thylaeodus*), which they closely resemble except for more regular coiling and the internal spiral lamellae. Scars of broken feeding tubes are common and may recur at regular intervals along the coil.

Assignable species :

P. (*M.*) *cereus* Carpenter, 1857. Philippines.

P. (*M.*) *cochlidium* Carpenter, 1857. Australia.

P. (M.) *complicatus* Dall, 1908. Panama Bay.

P. (*M.*) *flavescens* Carpenter, 1857. "Sicily" (evidently in error). Probably from West Mexico.
P. (*M.*) *floridanus* Olsson & Harbison, 1953. Florida, Pliocene to Recent.
P. (*M.*) *glomeratus* (Linné, 1758) [*Serpula*]. Mediterranean. (Synonym: *Vermetus subcancellatus* Bivona-Bernardi, 1832.)
P. (*M.*) *innumerabilis* Pilsbry & Olsson, 1935. Tropical West America.
P. (*M.*) *interliratus* Stearns, 1893. Cape Verde, West Africa.
P. (*M.*) *macrophragma* Carpenter, 1857 [type species]. West Mexico.
P. (*M.*) *mcgintyi* (Olsson & Harbison, 1953) [*Lemintina*?]. Florida, Pliocene to Recent.
P. (*M.*) *montereyensis* Dall, 1919. California.
P. (*M.*) *nerinaeoides* Carpenter, 1857. Australia.
P. (*M.*) *renisectus* Carpenter, 1857. Indo-Pacific.
P. (*M.*) *tokyoensis* Pilsbry, 1895. Japan.
P. (*M.*) *varians* (Orbigny, 1841) [*Vermetus*]. Caribbean.

Genus *DENDROPOMA* Mörch, 1861

Spiroglyphus of authors, probably not of Daudin, 1800; *Stoa* of authors, not of De Serres, 1846 (annelid); *Bivonia* Gray, 1847 [not Cocco, 1832]; *Siphonium* Mörch, 1859 [not Link, 1807]; *Magilina* Vélain, 1877 (?); *Vermitoma* Kuroda, 1928; *Veristoa* Iredale, 1937.

Solitary to colonial forms, corroding a trench in the substrate, in which the lower part of each volution is embedded; coiling planorboid in early whorls, becoming looser in later whorls, with a tendency toward right-angled turns. Colour of adult mostly white, variously stained with dark brown, especially within. Sculpture of lamellar growth-striae that may or may not be intersected by longitudinal lines, sinuous and rising toward a crest near the outer edge of the whorl in most species. Nuclear whorls two, dark brown in colour, inflated, smooth to malleated or axially ribbed, the apertural lip pointed or claw-like in some species. Operculum well developed, as large in diameter as the aperture, its inside surface having a distinct central attachment-scar that is somewhat button-like, its outside composed of chitinous plates in a spiral arrangement, either compactly welded to form a smooth surface or variously agglutinated with foreign materials.

Subgenus *DENDROPOMA*, *s. s.*

(Text-figs. 26–29)

Mainly solitary forms, minute to large, burrowing in other shells or in coral, rarely attached to rock. Operculum concave in large forms, flattened in smaller ones, buff-brown to mahogany red in colour. Sculpture varying from weak transverse threads to heavy longitudinal rows of scales.

The largest specimen of *D. maximum* seen (at the British Museum [Nat. Hist.]), had attained a length of over 18 inches. This is very exceptional. A diameter of 22 mm. is not uncommon in the larger forms, however. *D. maximum* is the form cited by Yonge and others from the Great Barrier Reef under the incorrect identification of *Vermetus novae-hollandiae*, the latter being a *Serpulorbis*.

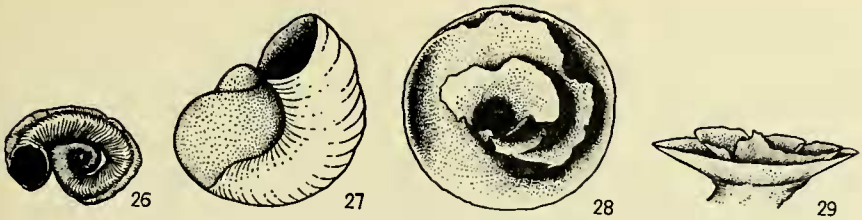

FIG. 26. *Dendropoma lituella*, sketch of lectotype, to illustrate manner of coiling. California. ×3. B.M. (N.H.) Reg. No. 195917.
FIG. 27. *D. lituella*, nuclear whorls. Stanford Univ. collection, southern California. ×25.
FIG. 28. Same, operculum, full view of a specimen with the membranous laminar surface exceptionally well preserved. ×10.
FIG. 29. Side view of same specimen.

Assignable species :
D. (*D.*) *andamanicum* (Prashad & Rao, 1933) [*Vermetus*]. Indian Ocean.
D. (*D.*) *corrodens* (Orbigny, 1842) [*Vermetus*]. Caribbean.
D. (*D.*) *leucozonias* (Mörch, 1861) [*Siphonium*]. West Africa.
D. (*D.*) *lituella* (Mörch, 1861) [type species : as *Siphonium*]. California.
D. (*D.*) *luchuanum* (Kuroda, 1928) [*Vermitoma*]. Japan.
D. (*D.*) *marchadi* Keen & Morton, 1960. West Africa.
D. (*D.*) *maximum* (Sowerby, 1825) [*Serpula*]. East Indies. [Lectotype in B.M. (N.H.).]
D. (*D.*) *nebulosum* (Dillwyn, 1817) [*Serpula*]. Caribbean.
D. (*D.*) *planorbis* (Dunker, 1860) [*Vermetus*]. Japan.
D. (*D.*) *rastrum* (Mörch, 1861) [*Vermiculus*]. California.

Subgenus *NOVASTOA* Finlay, 1927

(Text-figs. 30–33)

Colonial forms, usually encrusting rocks in honeycomb-like sheets. Nuclear whorls as in *Dendropoma, s. s.*, later whorls in tight, angulate coils spiralling upward from substrate. Operculum bright reddish brown, flattened to convex, the inner central mamilla conspicuous, the inner margin polished, the outer surface scaly.

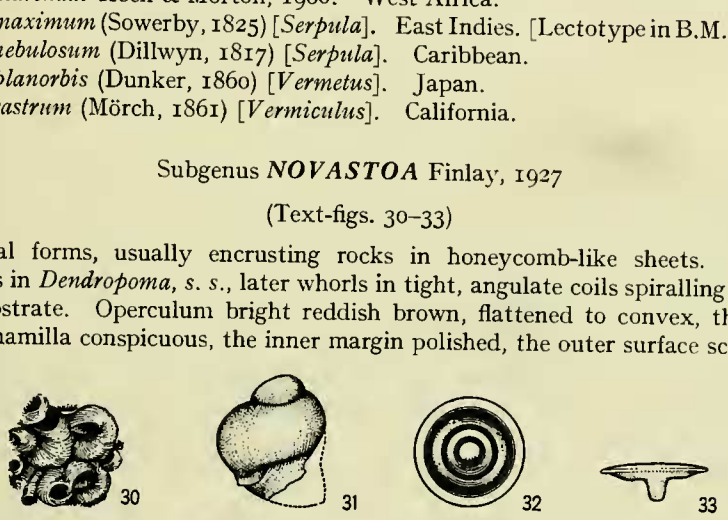

FIG. 30. *D.* (*Novastoa*) *lamellosum*. Detail of part of a colony. Stanford Univ. collection, from New Zealand. ×1·5.
FIG. 31. Nuclear whorls, redrawn, from Morton, 1951. ×25.
FIG. 32. Operculum, inner surface, showing the polished rim. After Morton. ×7.
FIG. 33. Same, side view, showing the large mamilla. ×7.

This group may be only situs forms, not a true genetic unit, for specimens in the dense clumps may be, to the eye, indistinguishable from solitary specimens as to operculum, nuclear whorls, and sculpture. Yet, when one compares such clumps from various geographic areas with the type species of *Novastoa*, one finds such a similarity of appearance as to suggest the usefulness of a subgeneric group name.

Assignable species :

D. (*N.*) *corallinaceum* (Tomlin, 1939) [*Vermetus*]. South Africa.
D. (*N.*) *ghanaense* Keen & Morton, 1960. West Africa.
D. (*N.*) *irregulare* (Orbigny, 1842) [*Vermetus*]. Caribbean.
D. (*N.*) *lamellosum* (Hutton, 1873) [type species : as *Siphonium*]. New Zealand.
D. (*N.*) *petraeum* (Monterosato, 1884) [*Bivonia*]. Mediterranean. (Synonym : *Vermetus glomeratus* Bivona-Bernardi, 1832 [not Linné, 1758].)
D. (*N.*) *tholia* Keen & Morton, 1960. East Africa.

Subgenus ***ELLIPTOVERMETUS*** Cossmann & Peyrot, 1922

The tube of the type species is ovate in cross-section, deeply immersed in a coral and showing lamellar growth-striae fluted by longitudinal ribs. Known only in beds of Aquitanian age (U. Oligocene) of France.

Assignable species :

D. (*E.*) *breigneti* (Cossman & Peyrot, 1922) [type species : as *Vermetus*]. French Aquitanian.

D. NOTES ON TYPE AND OTHER SPECIMENS

Vermetus adansonii Daudin, 1800

(Text-figs. 4–7)

V. adansonii Daudin, 1800 : 35.

Topotype material supplied by M. I. Marche-Marchad, of the Station de Biologie Marine de l'Institut Français d'Afrique Noire, provides at long last a firm basis for reappraisal of this type species. Concerning the locality M. Marche-Marchad says, (letter dated 20th December, 1954) : " Les exemplaires que je vous ai envoyés sont probablement des topotypes au sens le plus étroit du terme. En effet l'Ile aux Serpents = l'Ile de la Madeleine d'Adanson. C'est un petit îlot rocheux, très battu, situé à environ 2 milles à l'ouest du Cap Vert. Les 'bassins où l'eau de la mer est tranquille' et 'creusés naturellement dans le roc' (Adanson) n'abondent pas ; il n'y y en qu'un, c'est le 'lagon' d'où proviennent nos Vermets. Ce lagon n'a pas plus de 200 m. de periphérie et si ces mollusques ne viennent pas du rocher même ou Adanson les a observés—ce qui est probable—ils n'en sont certainement pas très éloignés! "

Fischer-Piette (1942) has figured Adanson's actual type material, rediscovered during the early part of World War II. The coiling of the shell is loose and rather irregular, and the medial whorls do not exhibit within any sign of the spiral laminae attributed to the species by Mörch. The present topotype specimens supply needed details as to the nuclear whorls (Text-fig. 5) and the operculum (Text-figs. 6–7).

A lectotype for *Vermetus adansonii* Daudin is here selected, the specimen of fig. 4, illustrated by Fischer-Piette on his pl. 9, fig. 3. It is in the collection of the Muséum National d'Histoire naturelle de Paris.

One concludes that the " crust " from Gaboon, equatorial Africa, identified by Mörch (1861 : 337) as *Vermetus adansonii*—which formed the concept of the species for many later authors—was not a true *Vermetus*. The latter seem to be rather more solitary forms than Mörch's description implies. His may have been the *Petaloconchus interliratus* Stearns, 1893 (a species based only on a type locality [Porte Grande, St. Vincent, Cape Verde, West Africa] and a vague description [" an elevated, threadlike ridge following the coiling spirally "]). Stearns' syntype material, cited by number (U.S. Nat. Mus. No. 125,378), is a tight colony of *Petaloconchus* (*Macrophragma*) with internal laminae well developed.

Vermetus (Vermetus) afer (Gmelin, 1791)

Serpula afer Gmelin, 1791 : 3745.

Fischer (1942 : 264) in refiguring Adanson's " Le Datin " suggested that it may be composite. Topotype specimens, however, taken by M. Marche-Marchad with the *V. adansonii*, match Fischer-Piette's figures well and seem to constitute a good species differing from *V. adansonii* by having rather regular planorboid coiling. This seems also to be more solitary. As a lectotype the specimen figured by Fischer-Piette on pl. 9, fig. 6 is here selected. It is in the Muséum National d'Histoire naturelle de Paris. The operculum of the topotype specimens is like that of *V. adansonii*.

Vermetus (Thylaeodus) contortus (Carpenter, 1857)

(Pl. 55, fig. 3)

Bivonia contorta Carpenter, 1857*c* : 305.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 57.6.4.1490. Mazatlán, Mexico.

Carpenter's best specimen was broken and his others considered to be young, which has led to misinterpretation of the adult form by later authors, including myself (Keen, 1958 : 298, fig. 200—a figure actually of an enigmatic *Serpulorbis*). However, Tryon (1886, pl. 49, fig. 27) seems to have figured it correctly. New material from near Mazatlán, collected by Mr. James McLean in December, 1959, affords opportunity to study a growth series taken alive. The adults are small (diameter of aperture about 2 to 3 mm.), the coiling somewhat less regular than that of the superficially similar *Petaloconchus* (*Macrophragma*) *macrophragma*. The colour is a warm wax-brown, and the sculpture is of longitudinal threads evenly beaded at the intersections of cross-threads, the whorls rounded in section, rarely rendered angulate by the lirae. Internal spiral laminae are completely lacking. A mature coil may be only 15–20 mm. in length. The two nuclear whorls are conic, moderately inflated, and pinkish brown in colour. The operculum has a spiral lamina that stands up from the cup ; the diameter is about half the diameter of the aperture.

This species is here selected as type of *Thylaeodus*. Previous allocation to *Bivonia* is untenable on two counts, as shown above (p. 193). The assignment to *Petaloconchus*—suggested by workers who discount the importance of the internal laminae in classification—although plausible as to form of operculum and nuclear whorls, would seem to broaden the limits of that group unduly. With a new insight as to the morphology of *Vermetus*, we can now suggest that this and a few related species could well form a subgenus under *Vermetus*.

Vermetus (Thylaeodus) indentatus (Carpenter, 1857)

(Plate 55, fig. 4)

Bivonia contorta, var. *indentata* Carpenter, 1857*c* : 307.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 57.6.4.1494. Mazatlán, Mexico.

In the lectotype, the longitudinal sculpture is heavier and less evenly beaded than in *V. (T.) contortus*. Coiling seems also to be less regular. The lectotype is dark brown in colour. A variant form, which may prove to be a separate species, is pinkish buff, with evenly cancellate sculpture. This species ranges more widely in the Gulf of California than does *V. contortus*.

Serpulorbis (Serpulorbis) arenarius (Linné, 1758)

(Text-figs. 12–13)

Serpula arenaria Linné, 1758 : 787. " Habitat in Indiis."
Serpulorbis polyphragma Sassi, 1827 : 484. Mediterranean.
Vermetus gigas Bivona-Bernardi, 1832 : 5, pl. 2, figs. 1–2. Mediterranean.

Linné's species is now generally considered to be the common large Mediterranean vermetid, better known under the name of *S. gigas*. *S. polyphragma* Sassi, type of *Serpulorbis* (see Text-fig. 14), seems to be only a smooth or unsculptured variant of the species. *S. arenarius* may form dense colonies of contorted tubes. Coiling of the young shell is planorboid. A report by Dr. Ottavio Priolo (1956*a*) gives evidence on the rapidity of growth : the hull of a boat sunk in a Sicilian harbour during World War II, raised in 1956, was covered with large masses of these shells. Specimens of these, sent to Stanford University, measure 13 mm. in diameter at the aperture and would be several inches long if the tubes were not contorted.

Serpulorbis (Serpulorbis) constrictor (Mörch, 1862)

Bivonia constrictor Mörch, 1862*b* : 63. Australia.

? Holotype : B.M. (N.H.) Reg. No. 195919.

Hedley (1913 : 294, pl. 18, fig. 71) figured this species with the statement, " In the British Museum is a single specimen, perhaps the type, but not so labelled . . . " Iredale (1937 : 254) considered that it is the type, which seems plausible.

Serpulorbis (Serpulorbis) eruciformis (Mörch, 1862)

(Pl. 54, fig. 3)

Thylacodes eruciformis Mörch, 1862*b* : 70. " California."

Holotype : B.M. (N.H.) Reg. No. 195915, on a *Crucibulum*. Probable type locality, the Gulf of California.

The type specimen consists of three whorls, with a beaded sculpture pattern. It measures about 30 by 35 mm. in total size.

Serpulorbis (Serpulorbis) squamigerus (Carpenter, 1857)

(Plate 55, fig. 5)

Aletes squamigerus Carpenter, 1857*a* : 226. Santa Barbara, California.

Syntype cluster : B.M. (N.H.) Reg. No. 55.3.14.57 (Nuttall Coll.) [*teste* S. P. Dance, 1959].

Carpenter himself in 1864 referred this to *Serpulorbis*, evidently realizing that it is not congeneric with *V. centiquadrus*. The sculpture varies from extreme scaliness to weak wrinkles, depending upon such factors as rapidity of growth, degree of crowding, etc. The geographic range is from Monterey, California, to southern Baja California. A similar and hitherto unrecognized species of *Dendropoma*, *D. rastrum* (see p. 207), occurs in the same area, distinguishable by the presence of an operculum and by a corroding habit. The two are doubtless confused in most collections.

Serpulorbis (?Cladopoda) oryzata (Mörch, 1862)

(Pl. 54, fig. 1)

Thylacodes ? oryzata Mörch, 1862*b* : 78. " China."

Holotype : B.M. (N.H.) Reg. No. 195912. Probably West Mexico.

Mörch correctly surmised that this shell in the Cuming collection had not come from China but from West Central America. It is a solitary form, with a few closely coiled whorls at first, and then coiling becomes not merely lax but obsolete, for the tube may stretch out in a weak curve for a distance of several inches. The white surface is rendered pebbly by intersecting striae, the longitudinal sculpture tending to twist spirally around the tube. A specimen in the Stanford University collection measures 250 mm. in total length, 15 mm. in diameter at the aperture. The geographic range seems to be between Guaymas and Acapulco, West Mexico. No living material was available for this study ; hence, the allocation of the species is highly tentative, especially as the shell has some points of resemblance both to *S. eruciformis* and to *Tripsycha tripsycha*.

Petaloconchus (Macrophragma) cereus Carpenter, 1857

P. cereus Carpenter, 1857*b* : 316, fig. 7. Philippines.

Holotype : B.M. (N.H.) Reg. No. 195920.

As Mörch commented, the type specimen is acid-etched and reveals a golden-yellow underlayer. The shell is regularly coiled and solitary, about 50 mm. in length. Some of the other British Museum specimens identified by Mörch show fine cancellate sculpture and appressed whorls.

Petaloconchus (Macrophragma) cochlidium Carpenter, 1857

P. cochlidium Carpenter, 1857*b* : 314, fig. 2. Australia.

Syntypes : B.M. (N.H.) Reg. No. 195921.

The syntype lot consists of a cluster of tightly coiled shells not unlike *P. flavescens* in appearance but dark brown in colour, with heavy lamellae, the upper double-keeled. Maximum diameter of the clump, 60 mm. ; length of one coiled individual, 20 mm. ; diameter of one tube, 1·2 mm.

Petaloconchus (Macrophragma) flavescens Carpenter, 1857

(Pl. 54, fig. 4)

P. flavescens Carpenter, 1857*b* : 314, fig. 3. "Sicily."

Syntype cluster : B.M. (N.H.) Reg. No. 195918.

As early as 1892 Monterosato pointed out that no such species is known in the Mediterranean, and it is not cited in the recent review of Sicilian vermetids by Priolo (1956*b*). However, anyone who has examined vermetids from the Guaymas-Mazatlán area of Mexico can recognize in this cluster a familiar form. The type lot having come from the Cuming collection makes its actual West American origin the more probable. Locally, the form is one of the commonest West Mexican vermetids. The *Turritella*-like tubes radiate outward in profusion, forming characteristically-shaped masses. The similar but much more loosely coiled *P.* (*M.*) *innumerabilis* Pilsbry & Olsson, 1935 (type locality, Tumbez, Perú) occurs also in the Guaymas-Mazatlán region, and only controlled laboratory studies will show whether the two are variants of a single species. The shells of *P. flavescens* vary in colour from terra-cotta to dark brown. Individual tubes are about 50 mm. in length, with a diameter at the aperture of 2 mm.

Petaloconchus (Macrophragma) lilacinus (Mörch, 1862)

Vermetus lilacinus Mörch, 1862*a* : 352. Zanzibar.

The type cluster of this form was from the Dunker collection, and may be in the Humboldt Museum, Berlin. Specimens of the "var. alpha" of Mörch, from Madagascar, are in the B.M. (N.H.) coll., Reg. No. 195922. They should probably best be considered hypotypes rather than syntypes. The shells are bright pinkish lavender, with weak laminae reduced to mere lirae in some tubes.

Petaloconchus (Macrophragma) macrophragma Carpenter, 1857

(Pl. 55, fig. 2)

P. macrophragma Carpenter, 1857*c* : 309. Mazatlán, Mexico.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 57.6.4.1500.

The specimen is attached to a *Muricanthus*. It is small, tightly coiled, dark brown, strongly sculptured, and with an internal lamina.

In a recent discussion of Carpenter's material by Palmer (1958 : 172), a printer's error in assembling type has introduced ambiguity, which the reader of Palmer's paper can resolve by transferring the last six lines of the text under *P. macrophragma* to precede the last paragraph of the page. (Also, the generic heading "*Aletes*" and the following seven lines should precede the discussion of *A. squamigerus* on page 173.)

Petaloconchus (Macrophragma) nerinaeoides Carpenter, 1857

P. nerinaeoides Carpenter, 1857*b* : 316, fig. 6. Australia.

Syntypes : B.M. (N.H.) Reg. No. 195923.

The syntype lot is a cluster that shows a few laminae. Carpenter's illustration seems somewhat exaggerated as to their strength.

Petaloconchus (Macrophragma) octosectus Carpenter, 1857

P. octosectus Carpenter, 1857*b* : 317, fig. 8. South Africa ?

Holotype : B.M. (N.H.) Reg. No. 195924.

Length of the 5 volutions is about 30 mm. The coiling is not distinctive, and the locality remains open to doubt.

Petaloconchus (Macrophragma) renisectus Carpenter, 1857

P. renisectus Carpenter, 1857*b* : 315, fig. 5. Oceano Indica ?

Type material was not detected at the B.M. (N.H.) upon search in 1958. The variety *P. r. woodwardi* Carpenter (1857*b* : 316), from an unknown locality, is represented by a compact cluster showing some laminae (B.M. (N.H.) Reg. No. 19595). Mörch (1862*a* : 348) described it as "forma 1".

Petaloconchus (Macrophragma) varians (Orbigny, 1841)

Vermetus varians Orbigny, in 1834–46 : 456, pl. 54, figs. 7–10. Rio de Janeiro.

Syntype cluster : B.M. (N.H.) Reg. No. 54.12.4.533.

Orbigny's figures (reprinted by Tryon, 1886, pl. 47, figs. 22–23) are good. The syntype cluster measures about 56 mm. high by 55 mm. across. Two opercula are glued on a separate slide. They are thin and chitinous but too crushed to show whether they had the characteristic upstanding spiral lamellae. The tubes have *Macrophragma* coiling, though internal laminae are not evident. They resemble the Floridan *P.* (*M.*) *nigricans* (Dall) but are larger in diameter.

Dendropoma (Dendropoma) corrodens (Orbigny, 1842)

Vermetus corrodens Orbigny, 1841–42 : 235. Orbigny, 1845–53 ? : 129, pl. 18, figs. 1–3.

Syntypes : B.M. (N.H.) Reg. No. 54.10.4.159. Cuba.

Several specimens constitute the type colony, burrowing on the spire of an *Astraea tuber*. Most of the specimens are white ; a few are brown. The operculum, on a separate mount, shows the internal mamilla or button. Diameter of a typical coil, 6·5 mm.

Dendropoma (Dendropoma) dacostae (Mörch, 1860)

Spiroglyphus dacostae Mörch, 1860*a* : 46. East Indies.

Holotype : B.M. (N.H.) Reg. No. 195925. Figured by DaCosta (1771, pl. 11, fig. 15) ; figure reprinted by Tryon (1886, pl. 55, fig. 9).

The specimen is attached to what looks like a block of marble but is probably part of a large shell, perhaps a *Cassis*, that has been cut to leave only the immediate base of the vermetid. Although the apical whorls are missing, their spiral trench shows that this is a close relative of *D. maximum*. At the large end the tube is only lightly attached. It is brown within. Some spiral and longitudinal sculpture may be made out, and the junction of the shell with the substrate is scalloped.

Dendropoma (Dendropoma) leucozonias (Mörch, 1861)

Siphonium (*D.*) *leucozonias* Mörch, 1861 : 155. West Africa.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 195926.

Solitary shells, with planorboid coiling, these are brown on the upper surface, white on the outer side of the whorl beyond the weak crest. Operculum red, conical, mamillate within. Diameter of a coil about 6·5 mm.

Dendropoma (Dendropoma) lituella (Mörch, 1861)

(Pl. 55, fig. 1)

Siphonium (*D.*) *lituella* Mörch, 1861 : 154. California.
? *S.* (*D.*) *megamastum* Mörch, 1861 : 153, pl. 25, figs. 12–13. California.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 195917, on *Haliotis fulgens*.

The syntype colony of *D. lituella* consists of a number of separated individuals burrowing and well entrenched in the cortical layer of the *Haliotis*. The brown juvenile shell has 1½ volutions. On the largest adult there is a slight crest. This shell measures 6 mm. in maximum length of coil. The operculum is in a separate vial ; it is flat, with a frayed edge.

Mörch gave no indication as to the collection from which his type specimens of *S. megamastum* came, but they are evidently not among the British Museum holdings, for no specimens bearing Mörch's labels were found there upon search in 1958. The form was described as shallowly burrowing in a *Haliotis*. Mörch thought that he saw bristles on the outside of the operculum, as in *Stephopoma* (hence, the choice of the name *Dendropoma*, meaning " branched lid "). Long and diligent modern

search having failed to bring such an operculum to light, it seems plausible to conclude that his supposed bristles were hydroid stalks or other agglutinated material on the scaly outer surface. Some specimens in the Stanford University collection have an operculum with tufts of sponge spicules that faintly resemble Mörch's sketches. Until his type specimens become available, it will be unwise to distinguish *D. megamastum* however much one would like to use the name for one of the two or more Californian vermetids that are clearly distinct from *D. lituella*.

Dendropoma (Dendropoma) platypus (Mörch, 1861)

Siphonium (*Stoa*) *platypus* Mörch, 1861 : 157.

Holotype : B.M. (N.H.) Reg. No. 195927. Hawaiian Islands, on a *Chama*.

The operculum, in place, is concave in form, as in *D. maximum*, which the shell resembles save that it is attached to another shell instead of being entrenched in coral. Mörch considered the operculum to be flatter than that of some others, but it now appears to be distinctly concave.

Dendropoma (Dendropoma) rastrum (Mörch, 1861)

(Pl. 54, fig. 2)

Vermiculus rastrum Mörch, 1861 : 180. No locality cited for shell.

Holotype : B.M. (N.H.) Reg. No. 195916.

The type material for this species is composite, consisting of a coarsely scaly, loosely coiling shell, without locality, and an operculum that Mörch assumed to have come from it. Other material that he had in hand, from Puntarenas, Costa Rica, probably influenced him in placing the species in *Vermiculus* (now *Vermicularia*). The operculum is not a vermetid operculum and probably is from a tropical West American *Vermicularia* (family Turritellidae). The shell itself, however, matches well a large form from California hitherto confused with "*Aletes*" *squamigerus* by Californian workers. It became evident that species representing two genera were masquerading under one name when, a few years ago, in the Stanford University collection, a *Dendropoma* operculum was observed in one tube of a cluster labelled "*A.*"*squamigerus*. Careful study of the entire contorted colony showed that the initial whorls were entrenched and *Dendropoma*-like in form and that the later whorls were a little corroded where one tube crossed another. Only a practised eye could distinguish the second species, so similar was the sculpture to that of *Serpulorbis squamigerus*. Mörch's holotype of "*V.*" *rastrum* corresponds perfectly with this otherwise nameless Californian form, and the recommendation is here made that it be regarded as probably Californian in origin, even though we lack the nuclear whorls and an authentic operculum to confirm unequivocally its position. None of the specimens available at Stanford University or in other collections studied have precise locality data, unfortunately, but the geographic range seems to be from central California southward to the northern part of Lower California. Specimens have been found attached in large clusters to soft rock as well as to such shells as *Haliotis*. Fully developed, the white tubes are heavy, as much as 10–12 mm. in diameter, and strongly sculptured with longitudinal rows of scales.

E. CHECK LIST OF WEST AMERICAN VERMETIDAE

It is to be hoped that with the aid of the clues given by this paper, other workers will undertake studies of the vermetids in areas of abundance. The present study was not begun with the intention of stressing any special geographic provinces, but as it progressed, one area became conspicuous for the occurrence of an unusual number of species and genera (with seven out of the presently-recognized ten generic units). A species list for this area—the west coast of North and Central America—seems appropriate, and it may serve as a start toward a more thorough review, which is now planned. The names of the species—most of which have already been mentioned—are arranged alphabetically, with original generic allocation, author, and date of proposal. Allocation in terms of the present classification is attempted (necessarily provisional for several forms); lastly, there are brief notes on the species not discussed elsewhere in this paper. [Generic names are abbreviated to initial letters, as follows: *D.*, *Dendropoma*; *P.*, *Petaloconchus*; *S.*, *Serpulorbis*; *V.*, *Vermetus*.]

albida, Bivonia, Carpenter, 1857. Nuclear whorls only, probably indeterminate. Holotype in B.M. (N.H.).

angulatus, Vermetus, Chenu, 1844, *ex* Rousseau MS. ?*SERPULORBIS*. No type locality stated; possibly not West American.

centiquadrus, Vermetus, Valenciennes, 1846. *VERMETUS, s.l.*, probably West Mexico.

compacta, Bivonia, Carpenter, 1864. *V.* (*THYLAEODUS*) (?). Type locality, Vancouver Island area.

complicatus, Petaloconchus, Dall, 1908. *P.* (*MACROPHRAGMA*).

contorta, Bivonia, Carpenter, 1857. *V.* (*THYLAEODUS*).

effusus, Vermetus, Chenu, 1844, *ex* Valenciennes MS. ?*SERPULORBIS*. No type locality stated; possibly not West American.

eruciformis, Thylacodes, Mörch, 1862. *S.* (*SERPULORBIS*).

flavescens, Petaloconchus, Carpenter, 1857. *P.* (*MACROPHRAGMA*).

imbricatus, Aletes? centiquadrus, Carpenter, 1857. Type specimen, B.M. (N.H.), probably indeterminate; juvenile.

indentata, Bivonia? contorta, Carpenter, 1857. *V.* (*THYLAEODUS*).

innumerabilis, Petaloconchus, Pilsbry & Olsson, 1935. *P.* (*MACROPHRAGMA*).

lituella, Siphonium, Mörch, 1861. *D.* (*DENDROPOMA*).

macrophragma, Petaloconchus, Carpenter, 1857. *P.* (*MACROPHRAGMA*).

margaritaceus, Vermetus, Chenu, 1844, *ex* Rousseau MS. *S.* (*CLADOPODA*).

margaritarum, Vermetus, Valenciennes, 1846. = *S. MARGARITACEUS*.

megamastum, Siphonium, Mörch, 1861. = *D. LITUELLA*.

montereyensis, Petaloconchus, Dall, 1919. *P.* (*MACROPHRAGMA*). California, from Monterey southward.

oryzata, Thylacodes?. Mörch, 1862. *S.* (*CLADOPODA*) (?).

panamensis, Vermetus, Chenu, 1844, *ex* Rousseau MS. *S.* (*SERPULORBIS*).

peronii, Vermetus, Chenu, 1844, *ex* Rousseau MS. *S.* (*SERPULORBIS*). No type locality stated; . possibly not West American. Not *V. peronii* of Valenciennes, 1846, which is probably *V. centiquadrus*.

rastrum, Vermiculus, Mörch, 1861. *D.* (*DENDROPOMA*).
squamigerus, Aletes, Carpenter, 1857. *S.* (*SERPULORBIS*). California and southward to southern Baja California.
sutilis, Bivonia, Mörch, 1862. ?*SERPULORBIS*. Holotype in B.M. (N.H.).
tripsycha, Vermetus, Pilsbry & Lowe, 1932. *TRIPSYCHA*.
tulipa, Vermetus, Chenu, 1843, *ex* Rousseau MS. *S.* (*SERPULORBIS*) (?). No type locality stated ; possibly not West American.

F. EVOLUTION OF THE VERMETIDAE

The earliest fossil that may possibly qualify as a vermetid is of Upper Cretaceous age. However, the preservation is not good enough to permit its unqualified acceptance as a gastropod. Some of the Lower Eocene fossils, from the Cuisian of France, are unquestionably vermetid, for they show clearly the scars of broken feeding tubes characteristic of several vermetid groups. The coiling of these shells suggests that of the genus *Serpulorbis*. Several similar species occurred in Europe during Middle and Upper Eocene time, and there were a few—perhaps only two—on the Gulf Coast of the United States. The genus continued to be represented throughout the Tertiary in Europe. By early Miocene time, *Petaloconchus*, with its internal spiral lamellae, had appeared in Europe as well as in the Caribbean area. *Dendropoma* is not so easily recognized in the fossil state, but *Elliptovermetus*, which seems to be an extinct subgenus of it, appeared in the Upper Oligocene of France.

We cannot trace directly the evolutionary history of nuclear whorls and opercula, as these are difficult or impossible to obtain fossilized, but some hint as to their pattern of development may be gained by a study of the range of form of these structures in modern vermetids, as shown in the various figures given here. The nuclear whorls of some *Macrophragma* species and some *Serpulorbis* are almost indistinguishable. This may represent the primitive form, away from which most of the groups have moved in different directions and to diffierent degrees, *Dendropoma* seeming to have diverged farthest. The same is true also for opercula. Hence, we may conclude that the evidence of the fossil record is at least not inharmonious with that derived from the study of living forms.

G. ACKNOWLEDGMENTS

During the more than twelve years since Professor T. A. Stephenson's first request for an identification set me to studying the Vermetidae, I have had much fruitful exchange of letters and ideas with Professor John E. Morton, whose paper will flesh out the bare bones of the present taxonomic treatment.

I wish to express to the officials of the British Museum (Natural History) my gratitude for the privilege of studying type material under their care and for permission to publish the photographs of several hitherto unfigured forms. These excellent pictures were made in the Photographic Section of the Museum. Mr. Peter Dance and Mr. Ian Galbraith, of the Mollusca Section, were especially helpful in making my stay worthwhile, and I appreciated their many thoughtful courtesies.

My debt to M. Igor Marche-Marchad has been mentioned above, for having

provided topotypes—taken alive—of (among others) the type species of *Vermetus*, from West Africa. I am indebted also to Mr. James H. McLean, student at Stanford University, for some topotypes from West Mexico. Grateful acknowledgment, too, should go to the many colleagues who have sent vermetid specimens for my study, such background material having been invaluable in a review of the whole family.

Line drawings used as Text-figures in this paper were prepared by Mr. Perfecto Mary, technician in the Department of Geology, Stanford University.

Two funds at Stanford University defrayed the costs of my trip to London in 1958, one supplied by an anonymous donor, the other from the Shell Oil Company's Grant for Scientific Research. Thus, I was privileged to handle the actual material studied a century ago by Carpenter and by Mörch, two authors of important systematic works on Vermetidae. More recently, an advantage came to me that neither of them had—first-hand study of these molluscs in an area where they are abundant. Through the kind auspices of the Belvedere Scientific Fund of San Francisco, California, I had a few days of observation and collecting at La Paz, Baja California, which afforded fresh insights into vermetid relationships and made a fitting climax to my several previous years of museum study.

For all this aid, so generously given, my thanks. One may hope that as a result, the Vermetidae will regain the esteem of malacologists and will not again be accorded a century of disregard.

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I. INDEX

PLATE 54

FIG. 1. *Serpulorbis oryzata* (Mörch). Holotype. British Museum (Nat. Hist.) Reg. No. 195912. ×0·7. Diameter of aperture, 15 mm.

FIG. 2. *Dendropoma rastrum* (Mörch). Holotype. B.M. (N.H.) Reg. No. 195916. ×1·3. Diameter of aperture, 9 mm.

FIG. 3. *Serpulorbis eruciformis* (Mörch). Holotype. B.M. (N.H.) Reg. No. 195915. ×1·3. Diameter of aperture, 7 mm.

FIG. 4. *Petaloconchus* (*Macrophragma*) *flavescens* Carpenter. Syntypes. B.M. (N.H.) Reg. No. 195918. ×2·6. Diameter of aperture, 1·5 mm.

PLATE 55

FIG. 1. *Dendropoma lituella* (Mörch). Lectotype (upper specimen), on *Haliotis*, the photograph retouched to block out a number of extraneous tubicolous annelids of the genus *Spirorbis*. B.M. (N.H.) Reg. No. 195917. ×4. Diameter of aperture, 1·5 mm.

FIG. 2. *Petaloconchus* (*Macrophragma*) *macrophragma* Carpenter. Lectotype (central specimen). B.M. (N.H.) Reg. No. 57.6.4.1500. ×3. Diameter of aperture, 1 mm.

FIG. 3. *Vermetus* (*Thylaeodus*) *contortus* (Carpenter). Lectotype. B.M. (N.H.) Reg. No. 57.6.4.1490. ×3. Diameter of aperture, approximately 3 mm.

FIG. 4. *Vermetus* (*Thylaeodus*) *indentatus* (Carpenter). Lectotype. B.M. (N.H.) Reg. No. 57.6.4.1494. ×3. Diameter of aperture, 1·5 mm.

FIG. 5. *Serpulorbis squamigerus* (Carpenter). Syntypes. B.M. (N.H.) Reg. No. 55.3.14.57. ×1. Diameter of aperture, 9 mm.